A statistical tool for identifying biological threshold responses to O_3 exposure or uptake

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Introduction

The generalized additive model (Hastie & Tibshirani 1990) was developed by statisticians nearly a decade ago, but its application in biological fields has occurred only in the last couple of years. Here we demonstrate its use in assessing the response of a sensitive biological attribute (carbon gain) to cumulative O_3 exposure or uptake. We chose carbon gain (gross photosynthesis) as the biological response attribute because it responds within a growing season to the stressors of interest (O_3, drought), and because it is linkable to total tree biomass via other models. However, a number of other biological response attributes could also be used (foliar injury as a single variable or in an index, tree biomass, wood production, etc). We used ponderosa pine because it is the most sensitive western US conifer to oxidant air pollution (Miller et al. 1983).

Ozone exposure indices for plants are based on the active growing season, hourly O_3 concentrations equal to or greater than a specified level, over a specified time (Stockton et al. 1997). Most exposure indices accumulate exposure over the entire growing season to correlate with biological responses. However, western forests commonly have a period of summer drought where stomatal conductance to water and O_3 is limited. Even in years with above-average precipitation with little change in predawn xylem potential, stomatal conductance declines after mid July when upper soil horizons dry. Because the statistical model can evaluate the effect of a single environmental stressor within the context of multiple stressors, we also evaluated whether drought stress was protective of, or deleterious to, carbon gain with accumulating O_3 exposure or uptake.

Using the general additive model, we assessed (1) at what value did cumulative O_3 exposure become deleterious to carbon gain at different sites; (2) whether cumulative O_3 exposure or uptake is a better metric for carbon gain; and (3) simultaneously tested the effect of the O_3 metric and drought stress in reducing carbon gain.

Approach

Seasonal gas exchange (net assimilation, dark respiration, stomatal conductance) was measured for twelve, statistically average 40-yr-old ponderosa pine trees in natural stands at each of four sites differing in pollutant exposure (and other factors) in three summers. O_3 concentration was measured on an hourly basis at each site, as well as other site microenvironmental factors. Because only 15% of the days during the growing season were foggy or cloudy, the model was very simple. The data from 1995 was used to develop first a model to predict stomatal conductance, and thus calculate O_3 uptake (Grulke et al. 2002a). The ability of the model to predict the measured gas exchange in a particular hour, on a particular day was tested in an average precipitation year (1993) and a 20% below-average precipitation year (1994): there was an excellent correlation. Another model was developed to then describe the seasonal changes in maxi-mum daily carbon uptake (net assimilation plus dark respiration losses at the same leaf temperature, or gross photosynthesis) (Grulke et al. 2002b) in response to the O_3 metric (cumulative exposure or calculated uptake) and drought stress (as determined from predawn xylem potential). Because the data was taken on monthly time steps, we used a locally weighted polynomial smoothing routine (Cleveland and Devlin 1988) to estimate the functional relationship of O_3 metric simultaneously with the other terms in the model. The data suggest the shape of the relationship between the explanatory variables and the response of interest.

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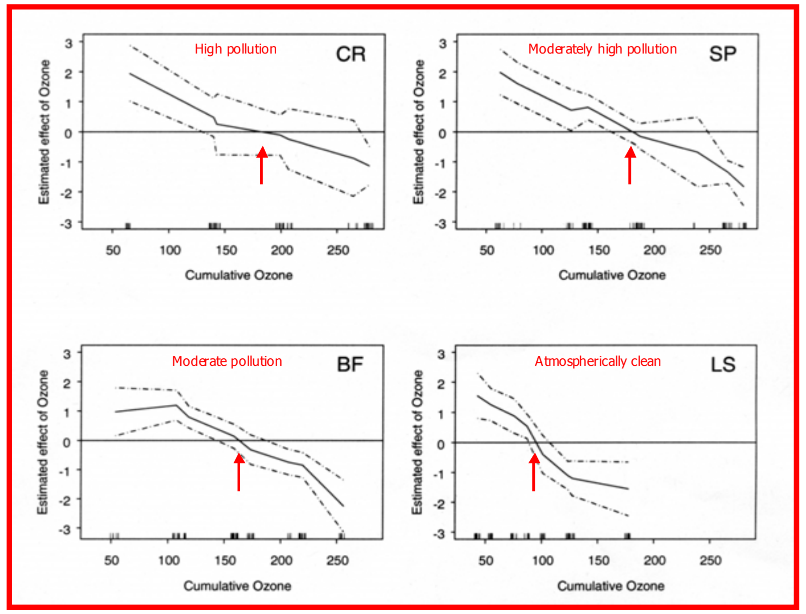


Estimated effect of cumulative O_3 exposure on CO_2 uptake

Holding the influence of the other environmental factors constant, cumulative O_3 exposure decreased CO_2 uptake across the full range of exposure (**figure left**). The zero line indicates the average CO_2 uptake rate of 12 trees at each site. When the response line was above the zero line, it suggested that CO_2 uptake was higher than the site average at the given value of the x variate (cumulative O_3 exposure). Conversely, when the response line was below the zero line, it suggested that the CO_2 uptake was lower than the site average at that value of the x variate. The dotted lines indicate the 95% confidence interval about the response line.

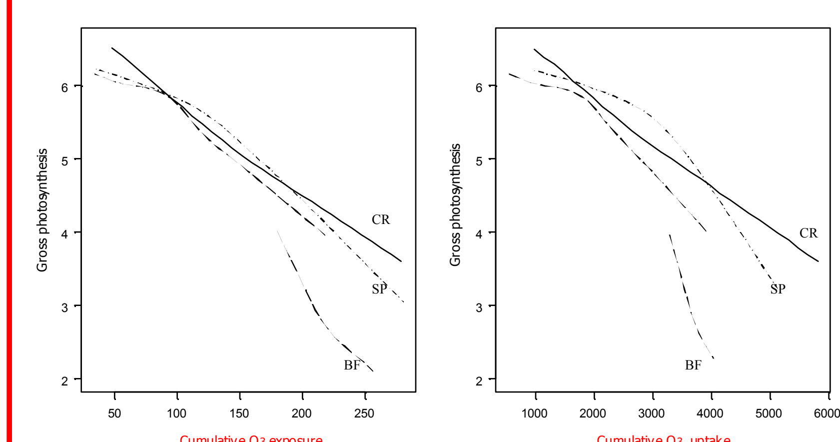
The response of CO_2 uptake to cumulative O_3 exposure at CR and SP was not significantly different, and the regression lines crossed the zero line at the same level of cumulative O_3 exposure: 180 ppm h. At BF, cumulative O_3 exposure < 100 ppm h did not affect the relationship between CO_2 uptake and O_3 exposure. However, between 100 and 210 ppm h, CO_2 uptake declined linearly with cumulative O_3 exposure. At BF, the line crossed the zero line at 160 ppm h. At Lassen, the response line cross the zero line at 90 ppm h cumulative O_3 exposure. The effect of late season drought stress was statistically significant ($p < 0.001$) only at Barton Flats. The percentages of explained variation at the four sites were 35% (CR), 54% (SP), 47% (BF) and 74% (LS).

Test of O_3 metric on CO_2 uptake

Gross photosynthesis for trees at all southern California sites declined linearly with cumulative O_3 exposure (**figure on right**). Drought stress and cumulative O_3 exposure combined to significantly reduce gross photosynthesis in late summer only at Barton Flats.

Gross photosynthesis for trees at Crestline and Barton Flats (non-drought conditions) declined linearly with cumulative O_3 uptake (**figure on far right**). Strawberry Peak had a non-linear decline with cumulative O_3 uptake, and the response differed significantly from that of Barton Flats ($p = 0.03$). Drought stress and cumulative O_3 uptake combined to significantly reduce gross photosynthesis in late summer at Barton Flats. Cumulative O_3 uptake was slightly better at explaining differences in the response of gross photosynthesis between sites.

Gross photosynthesis is in umol CO_2 m^{-2} s^{-1}. Cumulative O_3 exposure is in ppm h, and uptake is in mmol O_3 m^{-2} s^{-1}.



Conclusions

(1)Cumulative O_3 exposure was deleterious to CO_2 uptake at 180 ppm h at moderately high and high pollution sites, at 160 ppm h at a moderate pollution site, and at 90 ppm h at a relatively clean site. Cross-site comparisons can be made because the response line (CO_2 uptake to cumulative O_3 exposure) is relative to the population average CO_2 uptake rate *at that site*.

(2)Cumulative O_3 uptake appeared to be slightly better than cumulative O_3 exposure in distinguishing differences in carbon gain between sites.

(3)Late summer drought stress further reduced CO_2 uptake at only one site. The effect of drought stress was deleterious, not protective.

Ponderosa pine response to seasonal drought stress is very predictable and so are the seasonal trends in photosynthesis.

It is the most sensitive conifer in U.S. to O_3: a good species to model response.

Distribution of the species is shown in green, sites are marked in red.

	Lassen (LS)	Barton Flats (BF)	Strawberry Pk (SP)	Crestline (CR)
Pollution level	near pristine	moderate	moderately high	high
O_3 exposure, ppb h	38-42	62-64	69-76	79-80
N deposition, kg/ha yr	n.d.	9-Jun	n.d.	30-40
Soil N, % A_1, B_1	.01, .01	.08, .04	.11, .07	.20, .09
Annual ppt, cm	161	90	96	98
Predawn xylem in				
9/93, 9/94, MPa	-1.0, -1.1	-1.1, -1.7	-0.9, -1.6	-1.0, -1.7
Cumulative degree d	580, 680	1310, 1230	1980, 1820	2650, 2840
Growing season, d	88, 105	133, 78	113, 105	181, 170
Elevation, m	1700	1830	2240	1800

	LS	BF	SP	CR	*p*
Chlorotic mottle, %	1	8	19	24	0.001
Number of whorls	5.6	5.6	3.2	2.6	0.001
Needle length, mm	104	130	151	142	0.001
Branchlet length, mm	69	32	60	46	0.038
Branchlet dia., mm	4.7	5.7	5.1	5.6	0.410
Tree height, m	5.1	2.7	5	7.4	0.001
Bole diameter, cm	6.8	4.4	7.8	11	0.001

Table above: Summary of environmental variables at the four sites (see site locations on far right). These data are summarized from Kieffer and Fenn (1997), Grulke et al. (1998), and Grulke and Balduman (2000). **Table below**: Biological attributes of trees in used in this study. For foliar and branch attributes, previous year tissue in mid canopy was described.

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